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PREDICTING HABITAT RESPONSE TO FLOW USING GENERALIZED HABITAT MODELS FOR TROUT IN ROCKY MOUNTAIN STREAMS

T. K. WILDING[a,b]*, B. BLEDSOE[c], N. L. POFF[d] AND J. SANDERSON[e]

[a] *Colorado State University, Department of Biology, Fort Collins, Colorado USA*
[b] *Hawke's Bay Regional Council, Hydrology, Napier, New Zealand*
[c] *Colorado State University, Department of Civil and Environmental Engineering, Fort Collins, Colorado USA*
[d] *Colorado State University, Graduate Degree Program in Ecology, Fort Collins, Colorado USA*
[e] *The Nature Conservancy, Fort Collins, Colorado USA*

ABSTRACT

Dams and water diversions can dramatically alter the hydraulic habitats of stream ecosystems. Predicting how water depth and velocity respond to flow alteration is possible using hydraulic models, such as Physical Habitat Simulation (PHABSIM); however, such models are expensive to implement and typically describe only a short length of stream (10^2 m). If science is to keep pace with development, then more rapid and cost-effective models are needed. We developed a generalized habitat model (GHM) for brown and rainbow trout that makes similar predictions to PHABSIM models but offers a demonstrated reduction in survey effort for Colorado Rocky Mountain streams. This model combines the best features of GHMs developed elsewhere, including the options of desktop (no-survey) or rapid-survey models. Habitat–flow curves produced by PHABSIM were simplified to just two site-specific components: (i) *Q95h* (flow at 95% of maximum habitat) and (ii) *Shape*. The Shape component describes the habitat–flow curves made dimensionless by dividing flow increments by Q95h and dividing habitat (weighted usable area) increments by maximum habitat. Both components were predicted from desktop variables, including mean annual flow, using linear regression. The rapid-survey GHM produced better predictions of observed habitat than the desktop GHM (rapid-survey model explained 82–89% variance for independent validation sites; desktop 68–85%). The predictive success of these GHMs was similar to other published models, but survey effort to achieve that success was substantially reduced. Habitat predicted by the desktop GHM (using geographic information system data) was significantly correlated with the abundance of large brown trout ($p < 0.01$) but not smaller trout. Copyright © 2013 John Wiley & Sons, Ltd.

KEY WORDS: trout; velocity; depth; habitat; Rocky Mountains; generalized habitat model; PHABSIM

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INTRODUCTION

Flow regimes in the western USA and other semi-arid regions have been altered by the many dams and diversions constructed to meet water demands (Graf, 1999; WCD, 2000). The consequences for stream ecosystems have included the collapse of fisheries (Kareiva *et al*., 2000) and extinction of native fishes (Bestgen *et al*., 2006; Falke *et al*., 2011). Successfully managing flow alteration to prevent such impacts requires sound science that recognizes the broader physical constraints on ecosystems. The effects of flow alteration on fish populations depend on large-scale processes (e.g. temperature and flood frequency) that constrain the number of species surviving to respond to small-scale processes, such as water velocity at baseflow (Poff, 1997). Within this context, the importance of hydraulic habitat (depth and velocity) as a physical constraint is well established for trout in flowing waters, from observational and experimental studies at a range of scales (Bachman, 1984; Fausch, 1984; Jowett, 1990; Jowett, 1992).

Hydraulic habitat methods, such as Physical Habitat Simulation (PHABSIM), River Hydraulics and Habitat Simulation and River2D, predict the change in velocity and depth with flow, based on intensive surveys and calibrations of points in a stream reach (Annear *et al*., 2004). By comparing depths and velocities predicted by the hydraulic model to the observed depths and velocities used by trout [habitat suitability criteria (HSC)], these methods can generate *habitat–flow* curves [plots of the change in the weighted usable area (WUA) with flow]. These habitat–flow curves are not a prediction of trout biomass. Instead, they were developed to provide a better understanding of how the hydraulic habitat of trout changes in response to flow alteration, within the context of broader physical constraints (Milhous and Bartholow, 2006). A major hurdle for the implementation of conventional hydraulic habitat methods is the cost (Nehring, 1979; Estes and Orsborn, 1986; Souchon and Capra, 2004). This presents a barrier to

*Correspondence to: T. K. Wilding, Department of Biology, Colorado State University, Fort Collins, Colorado, USA.
E-mail: tkwilding@gmail.com

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carrying out such assessments, other than for large developments (e.g. dams or large diversions).

Flow management decisions are required for the vast majority of the stream network not regulated by large dams (e.g. for small run-of-river diversions). Poff *et al*. (2010) recognized the pressing need to develop regional-scale methods, based on data from reach-specific surveys, in order for science to keep pace with development. Generalized habitat models (GHMs) can help meet this need for regional coverage, as already demonstrated for some regions (Lamouroux and Capra, 2002; Lamouroux and Jowett, 2005; Booker and Acreman, 2007; Saraeva and Hardy, 2009a). Once developed, a GHM can reduce the survey effort needed to predict habitat–flow response, compared with additional PHABSIM or River2D surveys. The GHMs also make better use of prior knowledge of habitat–flow response, compared with rapid-survey methods, such as R2CROSS (Espegren, 1996). The steps in producing a GHM include the following:

(1) surveying hydraulic habitat to generate habitat–flow curves for a sample of stream reaches (e.g. using PHABSIM);
(2) fitting a function to the habitat–flow curve and extracting function components for each reach;
(3) using the observed sample of reaches to train a statistical model that predicts the components from selected predictor variables that can be obtained for many sites across a region with an acceptable level of effort; and
(4) generating habitat–flow curves for new reaches where predictor variables are known.

We reviewed existing GHMs to illuminate the best way forward. The GHM developed by Lamouroux and Capra (2002) successfully predicted habitat–flow curves (89% explained variance for adult brown trout), but predictions were based on reach attributes calculated from the intensive surveys (e.g. Froude number). The degree to which survey effort is actually reduced in applying the model to new sites remains in question.

More recent research has explicitly described the survey effort required for model implementation. For example, models by Booker and Acreman (2007) used watershed descriptors, or single-survey hydraulic data, to predict habitat–flow curves. The use of three unknown parameters for the habitat–flow function by Booker and Acreman (2007) produced a less parsimonious GHM that is more susceptible to parameter instability than functions used by Lamouroux and Capra (2002). Saraeva and Hardy (2009a) demonstrated the benefit of hydrogeomorphic classification in reducing the number of intensive studies required to make predictions. Their direct scaling of habitat–flow curves to 21 hydrogeomorphic classes achieved an area of application (3500 km^2 watershed) smaller than was achieved using statistical models elsewhere (e.g. France—Lamouroux and Capra, 2002; England—Booker and Acreman, 2007).

In this study, we combine the best features of previous models into one new GHM for the southern Rocky Mountains in Colorado. The resulting GHM provides a demonstrated reduction in survey effort with a desktop (remote-sensing data) and rapid-survey option (after Booker and Acreman (2007)), which minimizes the number of unknown function parameters (after Lamouroux and Capra (2002)) and exploits the hydrogeomorphic commonalities of the Rocky Mountains to reduce the number of intensive surveys required to train the GHM (after Saraeva and Hardy (2009a)). In addition, we used a similar approach to Saraeva and Hardy (2009b) for simplifying the PHABSIM predictions by omitting substrate cover and using per cent of maximum habitat rather than WUA. Our intention was not to replicate exactly the output from PHABSIM but to provide a biologically informative model that was developed and tested using the PHABSIM data. The successful interrogation of the habitat–flow predictions against observed trout abundance data therefore represents a vital step forward in demonstrating the validity of GHMs.

This article focuses on the *hydraulic habitat* (velocity and depth) of brown (*Salmo trutta*) and rainbow trout (*Oncorhynchus mykiss*) and how it changes with flow, recognizing that hydraulic habitat is one of several important constraints on trout populations (Milhous and Bartholow, 2006). The objective of this study was to develop GHMs for brown and rainbow trout that minimize data collection and maximize the area of application in Colorado using geographic information system data and easily obtained field measurements.

Success of the models was judged by two criteria: first, by better correlations with trout abundance than the Tennant (1976) method that provides thresholds based on per cent of mean annual flow (MAF) and, second, by demonstrating less survey effort than PHABSIM and River2D methods.

METHODS

The flow chart in Figure 1 summarizes the steps used to construct the GHMs for Rocky Mountain streams, with more detailed methods following.

Study sites

Data were obtained for 24 PHABSIM surveys in the Rocky Mountains to train the GHM (Table I). Survey data were obtained from the Colorado Division of Wildlife (Nehring and Anderson, 1993), HabiTech, GEI Consultants, Miller Ecological Consultants, Inc. and Stantec (Fleece, 2011). All but the Stantec survey were completed in the 1980s. Survey methods varied between sites to some extent, and

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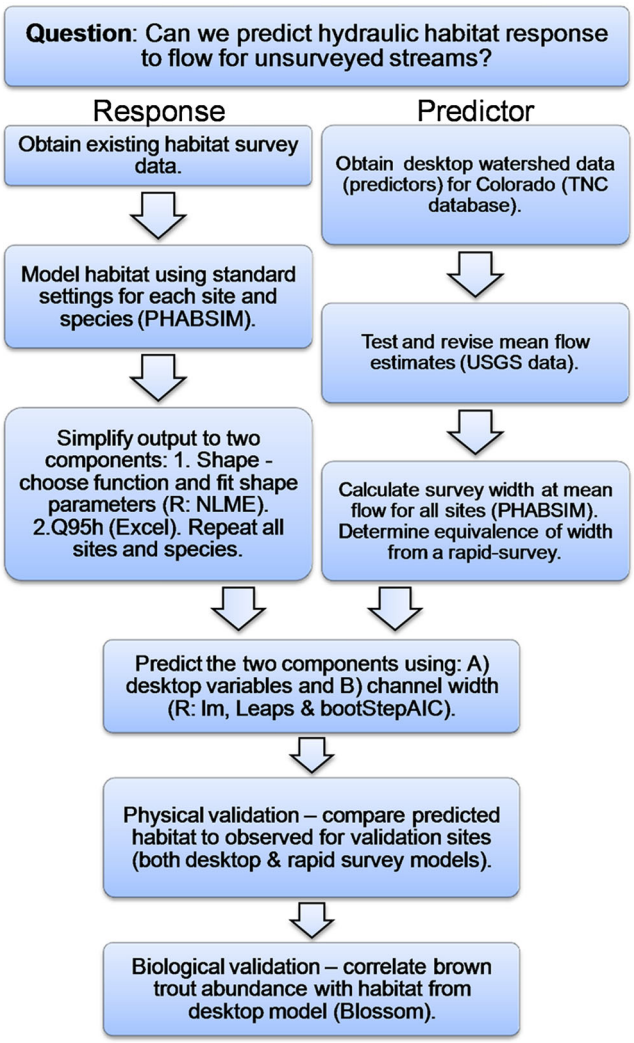

Figure 1. Flow chart summarizing our methods. The name of data analysis software is given in parentheses, including the name of packages implemented using R Project software. TNC, The Nature Conservancy; PHABSIM, Physical Habitat Simulation; NLME, nonlinear mixed effects

differences included the number of cross sections and the range of calibration flows (Table I). The impacts of dams and diversions provided the impetus for PHABSIM studies, with the actual surveys conducted further downstream in reaches supporting significant fisheries (e.g. Gold Medal fisheries).

To place the study sites in a broader physical context of regional-scale constraints (*sensu* Poff (1997)), site distribution was compared with all Colorado reaches (using data from NHDPlus). The probability of site occurrence was calculated using Maxent statistical software (Phillips and Dudík, 2008; Dudik *et al.*, 2010) with re-sampling from 20 875 Colorado reaches as background data (model area under the curve = 0.907). This demonstrated that site selection was biased to large, cool streams of Colorado, as depicted in Box 1. Most PHABSIM study sites had a temperature between 6 and 13 °C (annual average watershed air temperature) and a MAF between 1.8 and 14 $m^3 s^{-1}$ (the smallest site was 0.2 $m^3 s^{-1}$). The coincidence of popular coldwater fishing sites (State Wildlife Areas) with high probability reaches (>0.5) suggests that site bias reflects trout fishery bias. Snowmelt is the primary source of flow for these rivers (rather than rain), typically producing predictable timing of peak flows between late April and early July (class SN1 of Poff (1996)).

Desktop predictor variables

An initial set of desktop variables was retrieved from a geographic information system database provided by The Nature Conservancy for Colorado streams. Most attributes were sourced from NHDPlus (see www.horizon-systems.com). The database describes individual reaches that were delineated by tributary confluences, each with a unique identifier (COMID) and attributes. We selected a subset of attributes with expected mechanistic links to hydraulic habitat (Table II).

For the snowmelt streams of the Rocky Mountains, MAF is a useful metric of relative stream size that also represents flow magnitude during the warmest months. For example, flows for the Arkansas River (at USGS 07091200, 1989–2006) averaged 108% of MAF for August–September when temperatures averaged 92% of the annual maximum (of monthly means). Values of MAF for Rocky Mountain streams were estimated for NHDPlus using the equations from Vogel *et al.* (1999). This set of models uses watershed average precipitation and temperature calculated from PRISM data (Daly *et al.*, 1997), in addition to watershed area (i.e. the watershed upstream of each reach). Estimates of MAF were validated for our study using USGS gauge data (pre-diversion or reconstructed using diversion records). Estimates were generally close to the observed data; the exceptions being the Arkansas River and Cache la Poudre River, for which we developed revised water-balance models (described in Appendix 1 of Wilding (2012)).

Rapid-survey method

Rapid-survey GHMs can provide an intermediate level of assessment between a desktop GHM and a full PHABSIM survey. Width provides a measure of stream size that can be used in rapid-survey models. Because width varies with flow at a cross section, we chose the width at MAF as a standardized metric and modelled this in PHABSIM from survey data. The next step was to identify a rapid method for estimating width at MAF that required less survey effort than a full PHABSIM survey. The breakpoint width was estimated visually from plots of width versus average depth (breakpoint where width declines more rapidly towards zero) in a pilot study using 117 cross sections from 17 reaches in

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Table I. Site location, survey details and notable flow alterations for the study sites

River	Site	Dates surveyed	No. of XS	No. of Calibr.	Lat., long.	Notable flow alteration
Arkansas	Gold Medal Area	July 1985 to January 1986	8	3	38.510, −105.965	Receives transbasin water via Twin Lakes and Fry-Ark Project (1975)
Blue	Eagles Nest State Wildlife Area	Summer 1983	5	3	39.722, −106.125	Dillon Reservoir transbasin diverts out via Robert's Tunnel (1963)
Cache La Poudre	Lower wild trout water	February to August 1983	6	3	40.694, −105.255	Receives transbasin from Laramie Tunnel (1921), Grand (before 1934), Michigan (1905) and Wilson (1900) ditches; North Poudre Tunnel diverts out (1952)
	Below North Fork confluence	August and November 1986	6	2	40.698, −105.246	Receives transbasin from Laramie Tunnel (1921), Grand (before 1934), Michigan (1905) and Wilson (1900) ditches; North Poudre Tunnel diverts out (1952)
	Below the canyon mouth	August and November 1986	5	2	40.660, −105.209	Receives transbasin from Laramie Tunnel (1921), Grand (before 1934), Michigan (1905) and Wilson (1900) ditches. North Poudre Tunnel (1952) and Poudre Valley Canal divert out (1952). Upstream of CBT input (1957)
	Indian Meadows	Summer 1987	5	2	40.700, −105.541	Receives transbasin from Laramie Tunnel (1921); Grand (before 1934) and Michigan (1905) ditches
	Below Colorado Division of Wildlife Poudre Rearing Unit	Summer 1987	6	2	40.699, −105.705	Receives transbasin from Laramie Tunnel (1921); Grand (before 1934) and Michigan (1905) ditches
Colorado	Lone Buck	April to May 1983	6	3	40.048, −106.139	Grand Ditch (before 1934), Lake Granby (1949), Willow Creek Dam (1953), Windy Gap (1985) and Moffat Tunnel (1936) all with transbasin and divert out.
Dolores	Below McPhee Dam	July 1986	7	1	37.577, −108.587	McPhee Reservoir transbasin diverts out (1986); run-of-river diversion prior the 1800s
Fraser	Winter Park	1985	9	1	40.039, −105.881	Moffat transbasin diverts out (1936)
	Canyon	1985	6	2	39.942, −105.806	Moffat transbasin diverts out (1936)
Fryingpan	Old Faithful Station	August 1984 to November 1985	6	3	39.361, −106.841	Ruedi Reservoir (1968)
Gunnison	Black Canyon (Duncan-Ute Trail)	November 1982	6	3	38.669, −107.848	Uncompahgre Tunnel diverts out (1911); Blue Mesa Reservoir (1967), Crystal Reservoir, Morrow Point Reservoir
Lake Fork	Below Turquoise Lake	June 2010	5	4	39.219, −106.377	Receives transbasin from Busk–Ivanhoe tunnel (1925), Homestake tunnel (1968), Bousted tunnel (1972); Turquoise Reservoir 120 kAF (1968); Mount Elbert Conduit diverts out (1981).

(*Continues*)

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Table I. (Continued)

River	Site	Dates surveyed	No. of XS	No. of Calibr.	Lat., long.	Notable flow alteration
Little Vasquez	980 ft d/s Grand County diversion	1985	7	2	39.903, −105.795	Moffat transbasin diverts out (1936)
Middle Fork South Platte	Tomahawk Property	May to August 1983	6	3	39.080, −105.859	Receives transbasin from Arkansas River (1980)
North Fork Cache La Poudre	Upstream of Seaman Reservoir	July to August 1986	6	2	40.728, −105.236	Halligan Reservoir (1910)
	Downstream from Seaman Reservoir	July to September 1986	6	2	40.703, −105.232	Halligan Reservoir (1910) and Seaman Reservoir (1943)
North Fork South Platte	Below Foxton	Summer 1983	7	3	39.433, −105.227	Receives transbasin from Blue River via Roberts Tunnel (1963/6)
Rio Grande	Wason Ranch	July to October 1985	6	3	37.824, −106.894	Rio Grande Reservoir 54 kAF, (1914)
South Fork Rio Grande		May to July 1981	6	4	37.590, −106.729	Two small reservoirs
South Platte	11 Mile Canyon	Fall 1984	7	3	38.909, −105.461	Receives transbasin from Arkansas (1980), 11 Mile Reservoir and Spinney Mountain Reservoir
	Happy Meadow Campground	Summer 1983	9	3	39.014, −105.362	Receives transbasin from Arkansas (1980), 11 Mile Reservoir and Spinney Mountain Reservoir
Vasquez	1/4 mile d/s DC diversion	1985	8	2	39.901, −105.804	Moffat transbasin diverts out (1936)

XS, cross-sections; Calibr., calibrations; CBT, Colorado-Big Thompson project.

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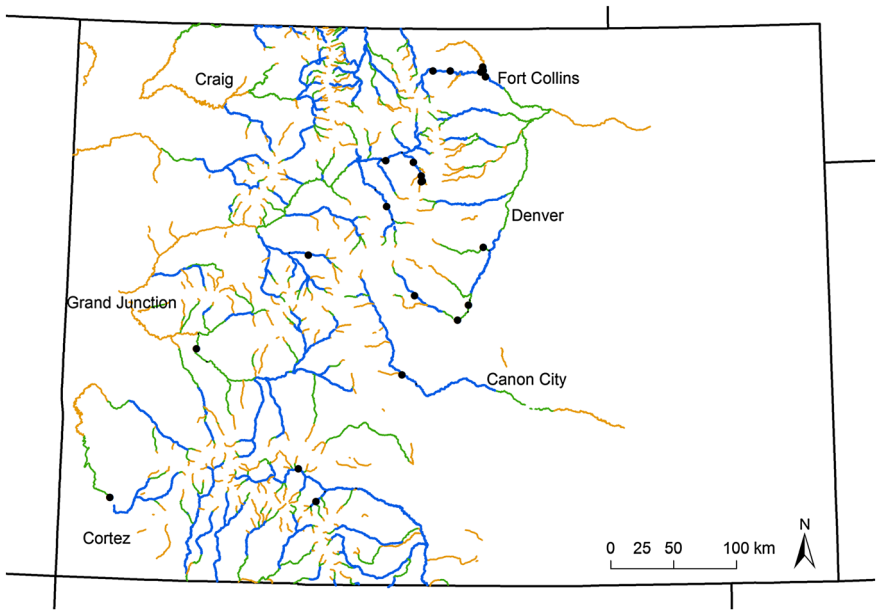

Box 1. Bias in site selection across Colorado based on temperature and mean annual flow, which translated to large, cool streams. The coincidence of popular coldwater fishing sites (State Wildlife Areas) with high probability reaches (>0.5) suggests that site bias reflects trout fishery bias. Three probability classes are displayed (blue 0.5–0.75, green 0.35–0.5 and red 0.2-0.35). Physical Habitat Simulation sites are illustrated as black dots

Colorado's Rocky Mountains (see Appendix 2 in Wilding (2012) for more description). Estimating the breakpoint width only requires survey data from one site visit with no velocity measurements, so it is more rapid than PHABSIM.

For physical validation sites lacking cross-sectional data, the rapid-survey width was instead measured as the visibly wet or unvegetated channel from aerial photographs in Google Earth (10–20 cross sections randomly selected over the reach). This aerial photograph method is further described in Appendix 4 of Wilding (2012).

Hydraulic modelling

We remodelled all 24 of the existing PHABSIM surveys using PHABSIM software (Windows version 1.20; Waddle, 2001) in pursuit of consistent model settings across sites. Some deviations were necessary for sites where different survey methods were used. Water surface levels were modelled using stage–discharge relationships (STGQ model using log–log linear regression) if calibration data were available and adequate (water surface profile models were necessary only for the Dolores River and Fraser River Site #1). The smallest sites (Little Vasquez and Vasquez) were removed at this point because the calibration of ratings was not adequate at higher flows, leaving 22 PHABSIM surveys to train the GHM. In PHABSIM, velocity was predicted using Manning's *n* values for each survey point at each flow increment (VELSIM in PHABSIM). Velocity adjustment factors (VAF IOC 11) were used to adjust observed Manning's *n* values for reduced roughness as depth increases. We wanted

Table II. Description of selected desktop variables developed by The Nature Conservancy* and NHDPlus+ for Colorado streams

MAF+	Mean annual flow ($m^3 s^{-1}$) natural estimate; Ln($x+1$) transformed and coded "In.maf1".
MAF Alt.*	Per cent flow alteration from transbasin diversions (quantified in HydroBase at http://cdss.state.co.us, accessed last 2008) plus predicted agriculture consumptive use [acre feet calculated as irrigated acres times 1.85 (Arkansas), 1.54 (Colorado), 1.45 (Dolores), 1.79(Gunnison), 0.83 (North Platte), 1.75(Rio Grande), 1.75 (South Platte) or 1.17 (Yampa)]
Elevation+	Reach-average elevation of blue line (m) and coded "elevtn".
Reach slope+	Slope of blue line over the reach (% slope = $100 \times m\,m^{-1}$); Ln(x) transformed and coded "In.gradR".
Watershed slope+	Slope of blue line averaged over the watershed (% slope) and coded "gradWS"
Dam storage density*	Reservoir storage volume/total annual runoff ($m^3 m^{-3}$); Ln($x+0.1$) transformed and coded "In.dam_stor0.1"; Reservoir volume data from the National Inventory of Dams were manually checked against alternative sources.
Riparian width*	Modelled width of flood influence (km); Ln($x+0.001$) transformed, and coded "In.rip_width.001".

Transformations for subsequent analysis are also detailed, with addition of values smaller than 1 (as in Ln[$x+1$]) necessary to normalize data with small non-zero values.

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to model specific habitat increments in order to train the GHM at flows less than maximum habitat; however, PHABSIM predicts hydraulic habitat at the flow increments (not the habitat increments) that are nominated by the user for each site. Obtaining the desired increments (maximum habitat, 95% of maximum habitat, plus nine increments at lower flows) therefore necessitated iterative remodelling and some interpolation between flow increments.

Selection of habitat suitability criteria

The PHABSIM uses HSC to convert predicted depths and velocities to hydraulic habitat. Separate GHMs were produced for the HSC selected for this study to represent brown and rainbow trout (Figure 2). A full description of the testing and derivation of all HSC is provided in Wilding (2012). The 'Cheesman' HSC (Thomas and Bovee, 1993; Shuler and Nehring, 1994) for adult brown and rainbow trout (BT2 and RT2) were modified by increasing the suitability of deep water to 1 (at deeper than optimum), because our re-analysis indicated that low catch rates in deeper water were an artefact of the rarity of deeper pools. This re-analysis used Maxent (Phillips and Dudík, 2008; Dudik *et al*., 2010) to better contrast the occupied habitat (presence) with the sampled habitat (target-group background) and avoid interpreting absences as avoidance. Maxent was also used to develop new HSC for this investigation, with trout separated only by size guild (juvenile T1 or adult T2) rather than by species. The new HSC were based on the same trout observations that were used to develop the Cheesman HSC plus data from the Cache la Poudre River (both described in Thomas and Bovee (1993)). Juvenile trout were 7–17 cm (assumed age of 1 year) and adult trout ≥17 cm (assumed age of 2+ years) (Thomas and Bovee, 1993).

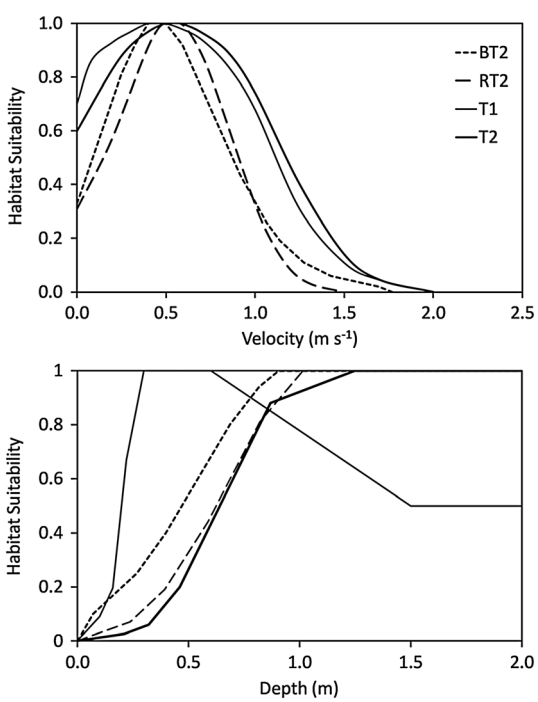

Figure 2. Habitat suitability criteria (HSC) for velocity and depth (*y*-axis standardized to maximum suitability of 1). The Cheesman HSC for adult brown and rainbow trout (BT2 and RT2) were modified from Shuler and Nehring (1994). The size-guild HSC were developed for this investigation, with trout separated only by life stage (juvenile T1 and adult T2) rather than by species (as described in Wilding (2012))

In an effort to simplify and improve the GHM, substrate and cover were not included as components of habitat suitability. A pilot study using data from 107 cross sections from the Cache la Poudre River (Gard, 2005) supported omitting substrate/cover, as it had little effect on the habitat–flow curves after standardizing hydraulic habitat by the maximum WUA (mean absolute deviation 2.8% of habitat between substrate off and substrate on for juvenile rainbow trout, paired *t*-test $p = 0.28$, $n = 26$). This is consistent with Ayllón *et al*. (2011), who reported substrate/cover had more effect on habitat magnitude (WUA) than on the shape of the habitat–flow curves. Note that the 11 PHABSIM surveys used for the physical validation of the GHM retained substrate/cover in the HSC. Therefore, the reported GHM prediction error includes any real change in substrate suitability with flow. Several species and life stages were not included in the Colorado GHM, including substrate-dependent spawning habitat, because the GHM is not intended to comprehensively portray the ecosystem response.

Modelling generalized habitat

With the aim of generating habitat–flow curves for unsurveyed streams of the Rocky Mountains, we decomposed the habitat–flow curves produced by PHABSIM into three components:

- *Q95h*—flow providing 95% of maximum habitat (at flows less than maximum habitat).
- *Shape*—the shape of the dimensionless habitat–flow curve. Habitat was converted to a per cent of *Maximum Habitat*, and flow was converted to a per cent of the Q95h.
- *Maximum Habitat*—maximum WUA.

The first two components, Q95h and Shape, are expected to be most useful for flow management, when used together. By omitting Maximum Habitat (third component), the modelling burden is reduced while still producing informative relationships for flow management.

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Q95h component. For Q95h, we chose the flow at 95% of maximum habitat as the flow metric, because it was less variable than the logical alternative of 100%. The point of maximum habitat can be poorly defined, with a wide range of flows offering close to maximum habitat (reflecting surveyed river morphology and the HSC used). The selection of 95% was based on another pilot study (Cache la Poudre River data from Gard (2005)), comparing 50 subsamples of six cross sections randomly selected from the 'population' of 107 cross sections. The standard deviation of these replicates was nearly halved by using the flow at 95% instead of 100% (standard deviation $1.17\,\mathrm{m^3\,s^{-1}}$ for 100% and $0.60\,\mathrm{m^3\,s^{-1}}$ for 95%, analysis of variance $p < 0.001$, $F = 250$, $n = 50$).

Shape component. A dimensionless Shape function was selected for each reach using the better fitting of two functions—quadratic or exponential. The vertex form of the quadratic equation ($y = A[x + B/2A]^2 + y_{\max}$) was used because $y_{\max}$ was known (i.e. 95% of maximum habitat provides the y-coordinate of a known turning point).

$$\text{Quadratic function:} \quad HV_{ij} = A\left({}^{Q_{ij}}/_{\mathrm{Q95}h_i} + {}^{B_i}/_{(2A)}\right)^2 + 0.95 + \varepsilon_{ij}$$

where subscript i denotes the individual reach and subscript j denotes the individual flow increments for each reach. The dimensionless response variable HV is the hydraulic habitat value, expressed as a proportion of maximum habitat. The independent variable Q is the flow, divided by Q95h to represent dimensionless flow (Q must be constrained to values less than Q95h, because HV is underestimated at higher values). Improved model performance was achieved by allowing B to vary across the reaches (cf. assuming $B/2A = x_{\max} = 1$), together with a fixed value of A.

The second function is a modified version of the exponential function from Lamouroux and Jowett (2005) (their Model 2).

$$\text{Exponential function:} \quad HV_{ij} = 1 + C_i.\exp\left(K.{}^{Q_{ij}}/_{\mathrm{Q95}h_i}\right) + \varepsilon_{ij}$$

Each function uses one fixed parameter (A for quadratic; K for exponential) fitted across all reaches in the hydrogeomorphic region and one reach-specific parameter (B or C). The parameters for each function were fitted simultaneously using a nonlinear mixed effects model (NLME) package (Pinheiro *et al.*, 2009; implemented using R, version 2.11.1). The NLME method estimates parameters that maximize the log likelihood (see Lindstrom and Bates (1990) for NLME model formulation and computational methods). Having just one reach-specific parameter (the 'random' parameter in NLME) provides a more parsimonious GHM, avoids parameter instability, and isolates the response of Shape to morphological drivers. Both the quadratic and exponential functions were parameterized over a range of Q/Q95h from 0.1 to 1, aiming for 10 data points per site and even distribution over the Q range.

The Bayesian information criterion (BIC) statistic (Schwarz, 1978) was used to determine which of the two functions provided a better fit to the data for each species and life stage (i.e. model with the lowest BIC score), in addition to reviewing plots of predicted versus observed values.

We therefore require two components to produce a habitat–flow curve for each site: Q95h and Shape (B or C for Shape, depending on which function is selected for the HSC). Therefore, the next step was to predict the two components using the desktop and rapid-survey variables. The predictor variables were transformed, if this improved normality, with appropriate transformations judged using histograms, Shapiro's statistic and normal Q–Q plots (width was square-root transformed; see Table II for other transformations). The two components were modelled using a multiple linear regression ('lm' function from the 'stats' package, implemented in R). The best model for each was judged on the basis of the best subsets analysis, which determined one combination of variables (from all possible) that produced the highest adjusted R^2 for each number of variables (calculated in R using the 'leaps' package; Lumley, 2009). The BIC was then used to determine *how many* variables should be included in the model (i.e. model with the lowest BIC score), comparing only the best subset models between each number of variables.

A bootstrap stepwise regression was then used to evaluate the stability of the variables, under re-sampling of the dataset, as this helps identify multicollinearity and strong outlier influences [calculated in R using the 'bootStepAIC' package, to optimize the BIC from 500 replicates; Rizopoulos, 2009]. Variable selection was reconsidered if selected in less than 70% of the replicate models. Residuals were also examined for the satisfaction of assumptions (Neter *et al.*, 1996), such as Q–Q plots for normally distributed residuals, and the F-statistics were checked (using the 'summary' function from the stats package in R). In most cases, there was an obvious best model that was supported by all statistics. Some level of judgement comes into play when the various methods provide conflicting results; in which case, we selected the model that could be best explained mechanistically.

Two models were produced for the HSC. The first was a desktop model based on the variables available for all stream reaches in Colorado (Table II). The second was a rapid-survey model using stream width plus the desktop variables (excluding MAF as a correlate of width), providing the option of more precise habitat predictions, where needed. For each of these models, an explained variance statistic was calculated to summarize model fit

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and was calculated as the R^2 value for predicted versus observed habitat values for each flow increment from combined reach data.

Validation

Both physical and biological validations were completed for the GHMs. The physical validation used independent PHABSIM studies (11 in total) for which only technical reports were available. These provided habitat–flow curves but not any survey data that could be remodelled using standardized PHABSIM settings and HSC. Most studies were completed by TetraTech for Grand County (8 out of 11, accessed at http://co.grand.co.us/GCHome/April-2008/Reach_Summaries/). The other three studies were carried out by Miller Ecological Consultants (Roaring Fork—Miller, 2009; Willow Creek—TetraTech reports, and Colorado River—Miller, 2008).

This comparison introduced new sources of error, including the HSC selected to represent trout (technical reports typically did not quantify the HSC used). Of the HSC that we used, the Cheesman HSC are likely to be more comparable with those used in the technical reports than the size-guild HSC developed for our study. The validation focused on the Q95h component, as it is more critical than the Shape component in determining the prediction success (coefficient of variation 55–63% versus 2–17% for Shape).

The biological validation compared predictions from the desktop models to trout abundance data obtained from the Colorado Division of Wildlife (wildlife.state.co.us/Fishing/Reports/FisherySurveySummaries accessed last July 2010). This provided data for trout at 24 sites on 12 streams in Colorado (sites likely biased to popular fisheries, access and suitability for fishing methods). This analysis focused on the number of fish per stream kilometre, because the alternative metric of fish per unit area effectively factors out the variable we are interested in—stream size. Data were available for two size classes of fish (>127 mm or > 356 mm). Brown trout were assumed to be better indicators of abiotic habitat, because rainbow trout populations have been decimated by whirling disease (Nehring and Walker, 1996). Annual fish monitoring results were averaged for 2008 and 2009. The *HV* was estimated at a flow of MAF/2, providing a measure of hydraulic habitat at a typical flow for the river. Quantile regression (Cade and Noon, 2003) was used to describe an upper bound for the biological validation because we expect hydraulic habitat to act as a constraint on trout abundance rather than the sole determinant of abundance (Dunham *et al*., 2002; Milhous and Bartholow, 2006). Blossom Software (Cade and Richards, 2007) was used to calculate a 90 percentile upper bound and an asymptotic rank-score statistic.

To compare performance with the desktop models, the correlation of trout abundance with the Tennant (1976) method was also analyzed. The Tennant method recommended thresholds for summer flow expressed as a proportion of MAF. To test the correlation of this method with trout abundance, the observed summer flows were divided by MAF for each site. We specified summer baseflows as the August–September mean (after Binns and Eiserman (1979)) and calculated the August–September mean over the trout monitoring period plus the 5 years prior (assuming 5 years since the conception of large trout). Summer flow data were obtained from nearby gauges (USGS and Colorado Division of Water Resources), with some adjustments needed for the differences in location (MAF was used to scale observed flows; Vogel *et al*., 1999).

RESULTS

Rapid-survey method

The breakpoint width, estimated from plots of width versus average depth for 117 cross sections, provided a close approximation of the width at MAF that was modelled from a full PHABSIM survey (breakpoint width = 0.983 * width at MAF, $R^2 = 0.975$). Estimating the breakpoint width only requires one site visit with no velocity measurements, and this represents a reduction in survey effort compared with PHABSIM.

For physical validation sites that lacked published cross-sectional data, the width of unvegetated channel was measured from aerial photographs. In a separate survey, this method provided estimates within 2 m of ground-surveyed bankfull width (see Appendix 4 in Wilding (2012)).

Modelling generalized habitat

The following sections describe the prediction of Q95h and Shape from the desktop and rapid-survey variables. The validity of the models is then described in terms of physical habitat predictions and correlations with trout abundance.

Q95h component. Models were developed to predict Q95h (flow at 95% of maximum habitat) for unsurveyed reaches. Of the desktop variables, MAF was included in all desktop models (best of all subsets) and stood up to bootstrap resampling (selected in >95% of replicate models; Table III). The MAF alteration was the only variable to reliably explain the residuals from MAF (reducing BIC for three out of four HSC). MAF alteration provides a measure of how flow and/or channel size may have changed from the natural condition to what is observed at present. The North Fork of the South Platte River was a major driver of this variable's selection, with the largest flow increase and the largest outlier from the MAF predictions (increase in channel width is visible from aerial photographs at the discharge point: latitude 39.461, longitude −105.676). The inclusion of MAF alteration in each model therefore depended on

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Table III. Model selection summary to predict the *Q95h* component for each species and life stage using desktop predictors

Species/life stage	BT2+		RT2+		T2+		T1+	
Parameter	Q95h		Q95h		Q95h		Q95h	
All subsets models:	BIC		BIC		BIC		BIC	
1 var	−64.0	ln.maf1	−64.7	ln.maf1	−55.2	ln.maf1	−51.1	ln.maf1
2 var	−64.9	ln.maf1 + maf_alt	−64.9	ln.maf1 + maf_alt	−54.6	ln.maf1 + maf_alt	−54.6	ln.maf1 + maf_alt
3 var	−63.0		−62.4		−52.2		−53.7	
4 var	−60.2		−59.7		−49.7		−51.6	
Bootstrap stepwise		%select		%select		%select		%select
variable selection	ln.maf1	99.8	ln.maf1	99.6	ln.maf1	97	ln.maf1	93.6
	maf_alt	66.2	maf_alt	57.2	elevtn	52.8	maf_alt	70.2
	ln.dam_stor0.1	44.2	ln.dam_stor0.1	39.4	maf_alt	50	ln.gradR	59.8
	gradWS	39.4	gradWS	37	ln.gradR	45.4	ln.rip_width.001	50.6
	elevtn	36.6	ln.rip_width.001	35.6	ln.rip_width.001	45.4	gradWS	49.4
	ln.rip_width.001	35.6	elevtn	31.4	gradWS	42.4	elevtn	47.6
	ln.gradR	27.6	ln.gradR	30.8	ln.dam_stor0.1	40.4	ln.dam_stor0.1	35.8
Final model	*Ln(BT2.Q95h + 1) ~ 0.6093 * ln. maf1 + 0.248 0* maf_alt + 0.5289*		*Ln(RT2.Q95h + 1) ~0.62001 * ln. maf1 + 0.22297 * maf_alt + 0.6860*		*Ln(T2.Q95h + 1) ~ 0.5886 * ln. maf1 + 1.0853*		*Ln(T1.Q95h + 1) ~ 0.51676 * ln. maf1 + 0.41369 * maf_alt + 0.60635*	
Model statistics								
MSE (MS resid)	0.0397		0.0397		0.0674		0.0634	
F-statistic	60.67		63.15		72.77		26.69	
Degree of freedom	2 and 19		2 and 19		1 and 20		2 and 19	
p-value, Pr(>F)	5.62E-09		4.042E-09		4.264E-08		3.034E-06	

The Bayesian information criterion (BIC) values for the best subset models are compared for each number of variables, up to four (lower BIC is better). The per cent of models that included each variable (under bootstrap re-sampling of the dataset) is given (%select). Model statistics are also given for the final selected model, if any variables were included. Variables and transformations are detailed in Table II (width was square-root transformed). MSE, mean square error; MS, mean square.

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including the North Fork. For this reason, MAF alteration was selected in less than 70% of replicate models for the three HSC, under bootstrap re-sampling of sites (Table III). But including the North Fork reinforced a subtle relationship that was visually apparent for the less altered sites, and the mechanism is clear behind this relationship with bigger flows increasing channel size.

The rapid-survey models outperformed the desktop models for the prediction of Q95h (BIC average −74 for rapid-survey, cf. −57 for desktop models; Tables III and IV). Width at MAF was the first variable selected for all four rapid-survey models and was the only variable selected for three of the models (BIC statistic increased with additional variables). Width provides a direct measure of channel size, and hence, MAF alteration did not feature as prominently in the width-based models (only included in the T1 model; Table IV).

Shape component. Of the two functions evaluated, the quadratic function provided a better fit to the data for the adult trout (RT2, BT2 and T2), producing smaller BIC values (quadratic $BIC < -1000$; exponential $BIC > -1000$), higher R^2 values (observed versus predicted $R^2 > 0.996$) and a visually better fit to the data (Table V). In contrast, the exponential function provided a better fit for juvenile trout with lower BIC values than the quadratic function for T1 and BT1 (Table V).

The Shape component was then predicted for the HSC (species/life stage) from the selected desktop and rapid-survey variables using multiple linear regression (Table VI). The Shape components did not vary markedly among sites (coefficient of variation ranged from 2% to 17% for the HSC), so it is perhaps not surprising that none of the HSC produced significant models (at $\alpha = 0.05$). The slope of the river channel was the most commonly selected predictor for Shape, with watershed slope included in models more often than reach slope (correlation between reach and watershed slope $R^2 = 0.01$).

An explained variance statistic was calculated to summarize model fit to the training data, combining Shape and Q95h across reaches for the HSC (R^2 value for predicted versus observed habitat values). The rapid-survey model achieved 82–89% explained variance (BT2 85%, RT2 83%, T2 68%, T1 72%; $n = 202$ to 234), and the desktop model 68–85% (BT2 89%, RT2 87%, T2 82%, T1 82%; $n = 202$ to 234).

Physical validation

Predictions of the GHMs were compared with 11 PHABSIM studies that were only available as technical reports. Plots of predicted versus observed Q95h indicate the general agreement for the two HSC that were compared (R^2 ranged from 0.84 to 0.96; Figure 3).

The rapid-survey models gave predictions that were closer to the observed values than the desktop models (median absolute difference for BT2 of 31% for rapid-survey versus 47% for desktop; and for RT2 14% for rapid-survey versus 40% for desktop). The desktop model consistently overestimated Q95h for the validation sites (Figure 3). Therefore, the rapid-survey model offers a worthwhile improvement over the desktop predictions. The width estimates used for most validation sites were actually measured from aerial photographs rather than the survey data. This was necessary because most technical reports only presented one cross section (exceptions—Roaring Fork and Colorado River CR7), and a sample of one is insufficient to calculate a reach-average breakpoint width.

The full model prediction (Q95h and Shape) was compared with the observed values for four randomly selected sites (Figure 4). This displays prediction success in a more familiar format of hydraulic habitat versus flow (akin to PHABSIM output). The predictions for Williams Fork BT2 had the largest departure from the observed Q95h (of all the validation sites and HSC) and therefore represent the worst-case scenario. Note that the full surveys offer alternative reach estimates, each limited in their approximation of truth by sample replication (Payne *et al*., 2004; Gard, 2005; Williams, 2009; Ayllón *et al*., 2011). Roaring Fork predictions improved drastically using the rapid-survey model, instead of the desktop model (Figure 4), indicating that the channel width is narrower than would be expected from MAF. Model predictions for the CR5 reach of the Colorado River compare favourably with both the PHABSIM survey at the lower end of the reach and the River2D survey at the upper end of the reach (Figure 4).

Biological validation

The abundance of all trout caught (>127 mm) was poorly correlated with both the BT2 and T2 predictions (Figure 5). This indicates that there are unmeasured population constraints. Some of these constraints might be revealed using hydraulic habitat at flow extremes (e.g. annual low flows and floods). At least we can say that the sites that supported the highest abundances of trout (>2000 trout km^{-1}) offered near-optimal habitat at the MAF (Figure 5).

In contrast, the abundance of large brown trout (>356 mm) was significantly correlated with the predicted habitat (Figure 6). High-value fisheries are distinguished by the abundance of large trout, so this is an important population metric. Both of the HSC for adult trout (BT2 and T2) were correlated with trout abundance. The T2 HSC were developed with better recognition of available habitat than BT2; however, the biological validation results did not reveal a better correlation with trout abundance using T2.

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Table IV. Model selection summary to predict the *Q95h* component for each species and life stage across the riverscape using rapid-survey width and desktop predictors (excluding mean annual flow). Otherwise, as per Table III

Species/life stage	BT2+		RT2+		T2+		T1+	
Parameter	Q95h		Q95h		Q95h		Q95h	
All subsets models	BIC		BIC		BIC		BIC	
1 var	−71.6	sqrt.width	−73.1	sqrt.width	−76.6	sqrt.width	−73.5	sqrt.width
2 var	−72.1	sqrt.width + ln. rip_width.001	−72.4	sqrt.width + ln. rip_width.001	−76.0	sqrt.width + ln. rip_width.001	−75.0	sqrt.width + maf_alt
3 var	−69.5		−69.7		−73.3		−74.6	
4 var	−67.2		−67.2		−70.5		−72.9	
Bootstrap stepwise variable selection		%select		%select		%select		%select
	sqrt.width	99.8	sqrt.width	99.6	sqrt.width	99.8	sqrt.width	99.6
	ln. rip_width.001	60.8	gradWS	42.4	ln. rip_width.001	49.4	maf_alt	81.2
	ln.dam_stor0.1	47.8	ln. rip_width.001	41.6	gradWS	47.2	ln.gradR	47
	gradWS	44.6	ln.dam_stor0.1	41.4	ln.dam_stor0.1	38.6	ln.rip_width.001	44.2
	maf_alt	40.6	maf_alt	27	elevtn	37	gradWS	38.8
	elevtn	22.4	ln.gradR	22.2	maf_alt	36.8	elevtn	35.6
	ln.gradR	21	elevtn	14.8	ln.gradR	36.4	ln.dam_stor0.1	30.2
Final model	*Ln(BT2.Q95h + 1) ~ 0.43295 * sqrt. width − 0.34712*		*Ln(RT2.Q95h + 1) ~ 0.44369 * sqrt. width − 0.22051*		*Ln(T2.Q95h + 1) ~ 0.467423 * sqrt. width + 0.003519*		*Ln(T1.Q95h + 1) ~ 0.39915 * sqrt. width + 0.20230 * maf_alt − 0.28918*	
Model statistics								
MSE (MS resid)	0.032		0.03		0.0256		0.0251	
F-statistic	154		172.6		224.5		81.81	
Degree of freedom	1 and 20		1 and 20		1 and 20		2 and 19	
p-value, Pr(>F)	7.508E-11		2.695E-11		2.454E-12		4.609E-10	

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Table V. Function parameters fitted for the quadratic and exponential functions using nonlinear mixed effects model

Function	BT2+	RT2+	T2+	T1+	BT1+
Quadratic					
Fixed A	−0.674	−0.697	−0.693	−0.635	−0.652
BIC	**−1174**	**−1030**	**−1209**	−920	−553
Log likelihood	598	526	615	471	286
R^2 (observed versus predicted)	0.9972	0.9966	0.9968	0.9884	0.9900
Exponential					
Fixed K	−2.492	−2.347	−2.349	−2.612	−2.615
BIC	−986	−733	−871	**−975**	**−592**
Log likelihood	503	377	446	498	306
R^2 (observed versus predicted)	0.9928	0.9827	0.9859	0.9914	0.9930

The Bayesian information criterion statistic (BIC) of the better fitting function is highlighted in bold (smaller BIC is better), together with other goodness-of-fit statistics. Fixed parameters (A and K) are given in the top rows.

How does the GHM compare with existing regional methods? The Tennant (1976) method is still commonly used (Reiser *et al*., 1989) and arguably offers the only alternative regional method for trout in the southern Rocky Mountains. The observed Tennant flow metric (August–September flow/MAF) was unable to explain much variation in the abundance of small or large brown trout (Figure 7). There may be an upper-bound response for trout >127 mm but only if the largest streams are excluded. The need to prune data indicates the limitations of the method, which incorrectly assumes that both small and large streams benefit equally from more flow. Note that calculating August–September flows to test the Tennant method required more effort to implement (sourcing and analyzing gauge records) than the Colorado desktop GHM.

DISCUSSION

We achieved our objective of predicting the response function between hydraulic habitat and flow for trout in unsurveyed streams, with the rapid-survey model achieving 82–89% explained variance and the desktop model 68–85%. The desktop models employed variables that are readily available for all Rocky Mountain streams to achieve better correlations with trout abundance than the Tennant (1976) method. In addition, the Colorado GHMs required less survey effort than PHABSIM.

An important step in achieving these objectives was reducing the standard PHABSIM output to just two site-specific components: the Q95h (flow at 95% of maximum habitat) and Shape for a dimensionless function. There was little variability in the Shape component, and hence, defaulting to the average parameter value worked in the absence of an adequate predictor.

Room remains for improvement in the Shape predictions, but this is less critical for the model's success than predicting Q95h (the observed coefficient of variation for Q95h was at least three times greater than that of the Shape component). In desktop models, the natural MAF (modelled using data from less altered rivers; Vogel *et al*., 1999) was an adequate predictor of Q95h, with small improvements achieved for most models by using the per cent alteration of MAF as a second predictor.

From the pilot studies, we observed that this combination of natural MAF and MAF alteration performed better than models that instead used existing flow. This is consistent with Williams and Wolman (1984), whose best model for bankfull width used both pre-dam (annual 1-day maximum) and post-dam (MAF) flow metrics.

If channel-forming flows were less altered than MAF, then existing channel morphology would not reflect the existing MAF. These channel-forming flows are typically much larger than MAF in cobble streams (e.g. Hey and Thorne (1986) used bankfull discharge). Even for snowmelt streams, such as those we studied, Ryan (1997) demonstrated that large reductions in MAF (20% to 60% reduction in annual yield) translated to small reductions in bankfull width, where the large floods remained intact (~12 year recurrence). There will be a relationship between natural MAF and channel-forming flows across the southern Rocky Mountains, unless large dams have altered the flood flow regime. Therefore, the parameters for MAF alteration should represent the autocorrelation between the alteration of MAF and the alteration of channel-forming flows (minus any temporal lag in channel adjustment; Petts, 1987).

The rapid-survey model provided better predictions of Q95h than the desktop model. Measured width represents the realized channel size, integrating the consequences of transport capacity (flow regime and slope), sediment supply and bank stability (Anderson *et al*., 2004; Flores *et al*., 2006). Width was not considered a desktop variable, as survey estimates of width at MAF (from PHABSIM) were used to train the model. The demonstrated reduction in survey effort comes from the strong correlation between width

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Table VI. Model selection summary to predict the *Shape* component for each species and life stage across the riverscape. Otherwise, as per Table III

Species/life stage	BT2+		RT2+		T2+		T1+	
Parameter	Quadratic B		Quadratic B		Quadratic B		Exponential C	
All subsets models:	BIC		BIC		BIC		BIC	
1 var	−153.0	ln.gradR	−134.2	ln.gradR	−107.0	gradWS	−83.9	gradWS
2 var	−151.8	elevtn + ln.gradR	−133.3	ln.gradR + gradWS	−108.7	gradWS + sqrt.width	−85.2	gradWS + ln.dam_stor
3 var	−149.0		−131.5		−108.2		−82.4	
4 var	−146.0		−128.9		−107.1		−80.4	
Bootstrap stepwise		%select		%select		%select		%select
variable selection	ln.gradR	61.4	ln.gradR	66	gradWS	82	gradWS	85.6
	elevtn	51.6	gradWS	55.4	sqrt.width	72.2	ln.dam_stor0.1	79
	ln.maf1	43.8	ln.rip_width.001	51.8	ln.rip_width.001	58.2	ln.maf1	61.2
	sqrt.width	39.6	sqrt.width	50.8	ln.gradR	55.4	sqrt.width	49.4
	ln.rip_width.001	38.6	ln.maf1	42	ln.maf1	54.2	elevtn	39.2
	gradWS	37.8	elevtn	41.6	ln.dam_stor0.1	54	ln.rip_width.001	38.4
	ln.dam_stor0.1	33.4	ln.dam_stor0.1	40	elevtn	44.4	maf_alt	35.4
	maf_alt	26.4	maf_alt	36.2	maf_alt	41.4	ln.gradR	35
	Null	0.8	Null	1	Null	0.8		
Final models	*quadratic B = 1.485*		*Quadratic B = 1.627881*		*quadratic B = 1.593605*		*expC = −0.8619854*	
Model statistics								
MSE (MS resid.)	0.0310		0.0465		0.0853		0.1454	
F-statistic								
Degree of freedom								
p-value, Pr(>F)								

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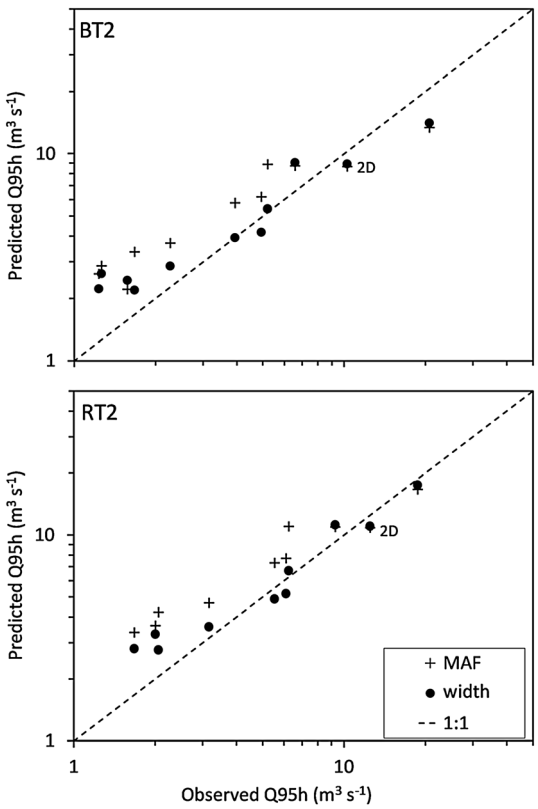

Figure 3. Predictions of *Q95h* (flow providing 95% of maximum habitat), comparing predictions from the Colorado generalized habitat models with the observed values from the independent Physical Habitat Simulation studies. Results for both the desktop (mean annual flow 'MAF') and rapid-survey models ('width') are presented for adult brown (BT2) and rainbow trout (RT2). Points would fall on the 1:1 line if the predicted values matched the observed. The R^2 for BT2 was 0.84 for desktop and 0.92 for rapid-survey; R^2 for RT2 was 0.90 for desktop and 0.96 for rapid-survey

at MAF (full survey) and breakpoint width (rapid survey) that approached a 1:1 relationship. Rapid-survey width is estimated from plots of width versus average depth, so it does not require velocity measurements or return visits. In addition, the success of rapid-survey models in predicting Q95h for validation sites was achieved using rapid-survey estimates of width (i.e. not using width at MAF from PHABSIM surveys). Surprisingly, the validation analysis indicated that the estimates of channel width from aerial photographs produced worthwhile improvements, compared with the desktop model. The use of aerial photographs introduces error at a cross section scale, but this error is offset at a reach scale with more cross section replicates, unlimited reach access and the ability to measure change in width over time from historical aerial photographs (see Marcus and Fonstad (2008)). Therefore, aerial photographs can alleviate some of the sampling and scale issues discussed by Dunbar *et al*. (2011) and Petts (2009). Better predictions are dependent on adequate aerial photographs for the stream of interest and are less useful for small streams where bank vegetation conceals the channel (see Bird *et al*. (2010)).

The desktop model overestimated Q95h for most validation sites. Given that two decades separate most of the training site surveys from the validation site survey (median year 1985 and 2007, respectively), perhaps this overestimation reflects a change in the relationship between a static estimate of MAF and a varying channel size (*sensu* Milly *et al*. (2008)). There is evidence that larger floods preceded the earlier surveys of training sites, increasing channel sizes. For example, the Yampa River (at USGS09251000) produced the highest 5-year mean flow on record for the period 1982–1986, compared with 2000–2004 that recorded the second lowest flow. The rapid-survey models are therefore expected to be more robust to global change than the desktop models.

In addition to the dynamic predictions of the GHM (habitat response to changing flow), the rapid-survey predictor (width) can also be dynamic (e.g. model change in width with change in peak flow using historical aerial photographs). This presents an opportunity for evaluating the habitat response to flow under some future scenarios of channel width (*sensu* Carpenter (2002)), which is not offered by PHABSIM (Petts, 2009). We can then take a step forward in our understanding but must add the uncertainty in how channel shape changes with width to the long list of uncertainties for the streams of tomorrow (see Brandt (2000) and 'Channel dynamics and stability' section in Bovee *et al*. (1998)). Neither the desktop nor the rapid-survey models assume static ecosystems. It is up to the investigator to decide if sustaining trout populations is a reasonable expectation for a given site (see Wenger *et al*. (2011)), as dictated by broader environmental constraints (Poff, 1997).

The predictive success that we achieved using the chosen methods compares favourably with the results of similar studies outside Colorado (Lamouroux and Souchon, 2002; Lamouroux and Jowett, 2005; Booker and Acreman, 2007; Saraeva and Hardy, 2009a). The New Zealand GHM by Lamouroux and Jowett (2005) achieved an explained variance of 73% for adult brown and 76% for rainbow trout. For France, Lamouroux and Capra (2002) achieved an explained variance of 89% for adult brown trout and 86% for juveniles.

The variance explained by the Colorado models (rapid-survey 82–89%, desktop 68–85%) approached the results achieved by Lamouroux and Capra (2002) and exceeded the results achieved by Lamouroux and Jowett (2005). But note that the explained variance from the Colorado model represents the end product, compared with Lamouroux and Capra (2002) and Lamouroux and Jowett (2005), whose values for explained variance exclude the added uncertainty of estimating width (i.e. they predicted habitat versus unit-width flow, not versus streamflow). It appears that a similar

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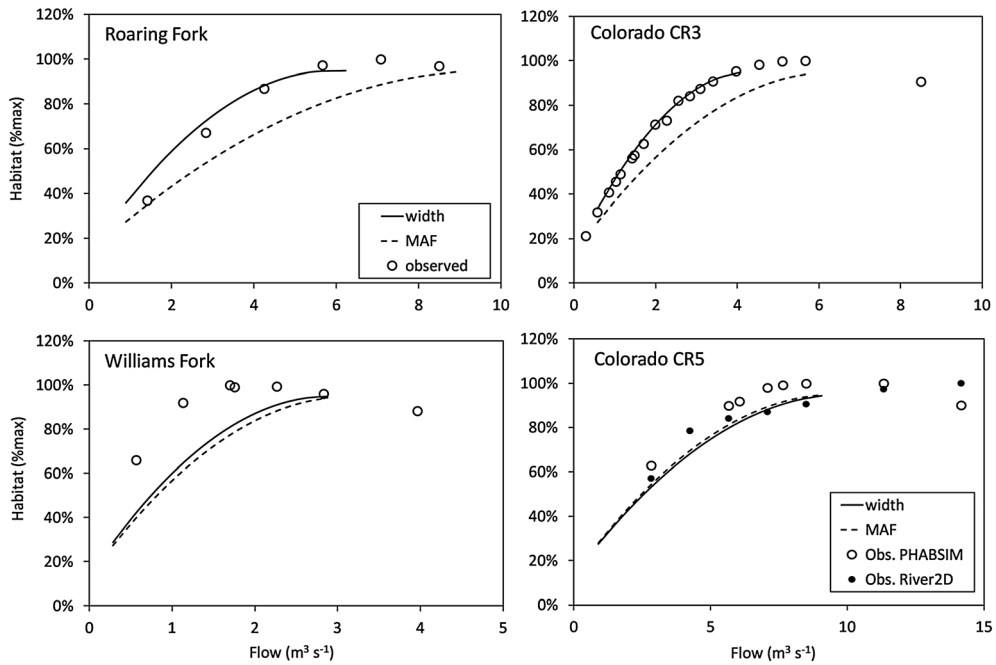

Figure 4. Habitat–flow response curves for adult brown trout (BT2), comparing curves predicted from the desktop (mean annual flow 'MAF') and rapid-survey models ('width') with the observed results from four surveys not included in the training dataset (compare the predicted lines with the observed points). For Colorado River site CR5, the observed results are presented from both a Physical Habitat Simulation (PHABSIM) survey and a River2D survey

level of success was achieved here using less training data and a demonstrated reduction in survey effort. We achieved a similar level of prediction success for the validation sites (mean 82% explained variance), despite estimating stream width from aerial photographs (as surveyed width data were unavailable).

The predictive success of GHMs for the Nooksack basin (Washington, USA) by Saraeva and Hardy (2009a) was evaluated using the root-mean-square error, for which they achieved values often less than 15% (evaluated against the training data). The equivalent root-mean-square error calculated from all the Colorado validation sites was 15% for BT2 and 18% for RT2. We attribute this success to focusing on just one region (southern Rocky Mountains), using dimensionless habitat (% of maximum), omitting substrate/cover and focusing on sub-maximal flows.

Biological validation demonstrated the strength of the Colorado GHM in explaining the number of large brown trout (>356 mm) per kilometre of stream. We believe this correlation provides an appropriate measure of validity. Trout abundance per kilometre of stream is an appropriate metric for evaluating WUA (square metre of habitat

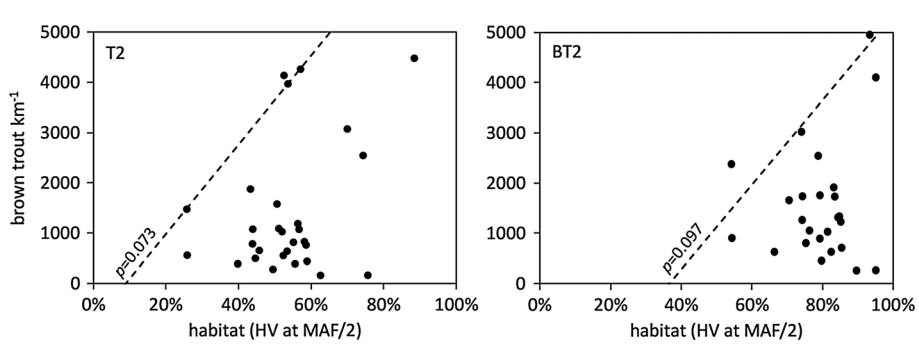

Figure 5. Number of brown trout >127 mm per kilometre versus the HV (hydraulic habitat value) at half the MAF (mean annual flow) predicted using the desktop generalized habitat model for size-guild adult trout (T2, left plot) and adult brown trout (BT2). Quantile regression was used to describe an upper bound (90 percentile and a *p*-value of asymptotic rank-score statistic calculated using Blossom Software; Cade and Richards, 2007)

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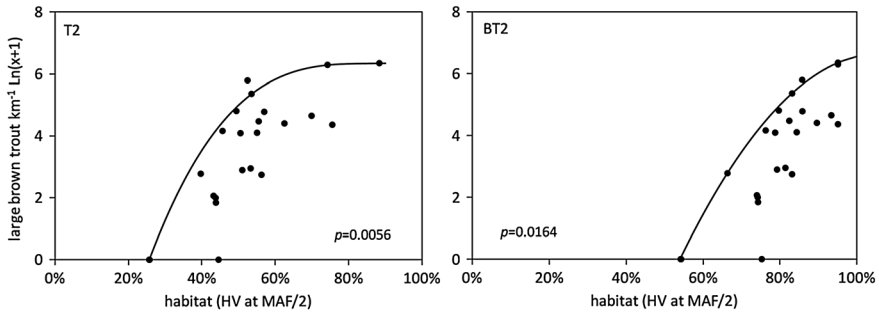

Figure 6. The abundance of large brown trout (>356 mm km^{-1} with log transformation) versus the predicted HV (hydraulic habitat value) at half the mean annual flow. Quantile regression was used to describe an upper bound (90 percentile and *p*-value of asymptotic rank-score statistic calculated using Blossom Software)

per kilometre), in contrast to HSC or %WUA that should be evaluated against trout density (number per square metre). The HV metric that we used was validated against trout per kilometre because the HV data were derived from WUA data (habitat per kilometre standardized by maximum habitat per kilometre). The correlation between trout density per square metre and HV was not significant.

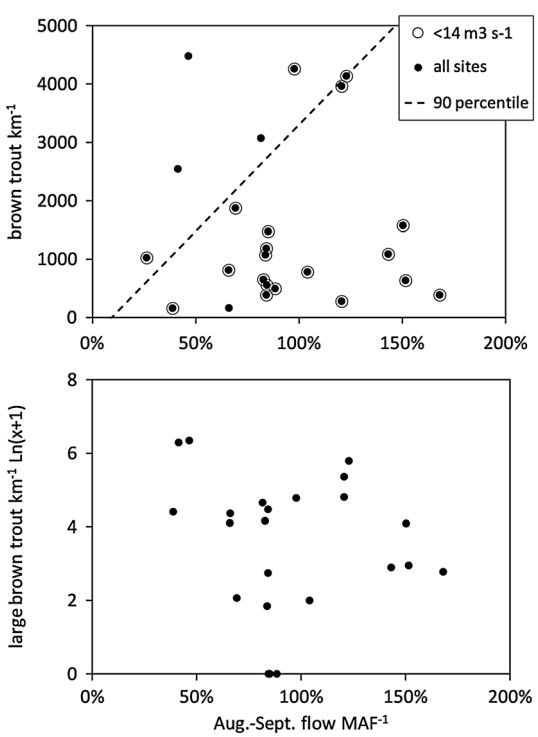

Figure 7. Brown trout abundance response to summer flow for all trout caught >127 mm (upper plot) and large trout >355 mm (lower plot). This is intended to compare the validity of the Tennant (1976) method using the measured August–September mean flow divided by Vogel mean annual flow (MAF). A quantile regression (90% percentile in dashed line) was performed excluding large streams (>14 m^3 s^{-1}) and excluding sites >125% of MAF (*p*-value of asymptotic rank-score statistic: 0.041)

The inclusion of small trout (127–356 mm) introduced substantial variability that the models could not explain. This suggests that hydraulic habitat is a primary constraint on a river's carrying capacity for large trout, but numbers of smaller trout are constrained by additional variables. For example, floods impact the number of juveniles (Nehring and Anderson, 1993; Latterell *et al*., 1998), and Hayes *et al*. (2010) suggested that self-thinning of juveniles in years with less flood disturbance can translate to inter-year stability of age-2 brown trout. The poor prediction for small trout might also reflect the more fundamental problem raised by Railsback *et al*. (2003), where the HSC were developed from juvenile trout forced into sub-optimal habitats by larger trout. Problems with juvenile HSC are further supported by the inferior fit of our Maxent HSC models for juvenile trout compared with adult trout (area under the curve values of 0.73 and 0.90, respectively; Wilding, 2012). The obvious way around this problem is to base the flow recommendations on adults rather than juveniles. This is a useful outcome, given that flow managers must ultimately choose a single flow value to apply at any point in time.

There are several important caveats worth mentioning. The GHMs were developed for Rocky Mountain streams of Colorado. There are many important differences to other regions that could invalidate the GHM (e.g. different relationship between MAF and channel-forming flows and different fish community). Within the Rocky Mountains, small steep streams were poorly represented in the dataset, so the models may produce misleading results for streams with an MAF less than 0.6 m^3 s^{-1} and reach slopes greater than 10%. Conservation populations of the native cut-throat trout (*Oncorhynchus clarkii*) are now largely confined to headwaters beyond the reach of introduced salmonids (Peterson *et al*., 2004), and such streams are poorly represented by the GHMs. The quadratic function for Shape will underestimate the habitat at flows greater than Q95h. Most caveats that apply to PHABSIM (see Annear *et al*. (2004))

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also apply to this GHM. For example, habitat–flow curves are not a prediction of trout biomass. Instead, hydraulic habitat is just one of several potential physical constraints (e.g. flood disturbance and temperature) that operate at different scales to determine population performance (Poff, 1997; Milhous and Bartholow, 2006).

Reaches surveyed for training and validating the model were selected to answer specific flow management questions rather than provide a random selection of Rocky Mountain streams. This was demonstrated in our Maxent analysis that revealed site bias to large, cool rivers. Even within the population of large, cool rivers, reaches were not selected randomly. We must therefore acknowledge the potential for statistical tests to underestimate the true error in applying the models to the population of Rocky Mountain streams.

Frameworks such as the Ecological Limits of Hydrologic Alteration (ELOHA; Poff *et al*., 2010) provide the context for the development and implementation of individual flow–ecology methods, such as this GHM, at a regional scale. The ELOHA framework formalizes the use of existing data to develop multiple flow–ecology methods for specific stream types that align with stakeholder objectives (see Kendy *et al*. (2012) and Sanderson *et al*. (2012)). Furthermore, New Zealand's proposed national standards for ecological flows spell out when GHMs can be used in place of intensive surveys, depending on instream values and flow alteration (see Appendix 4 in MfE, 2008). In the absence of such specific guidelines for Colorado, the GHM itself could be useful for deciding when to use intensive surveys (e.g. if the GHM predicts substantial reductions in habitat). The potential for developing more biologically relevant metrics from existing remote-sensing data using the Colorado GHM could also advance regional-scale niche modelling.

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